17(2)

17(2)

FISKERIDIREKTORATETS SKRIFTER

SERIE HAVUNDERSØKELSER

VOL. 17, No. 2

LIBRARY
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DIRECTORATE OF FISHERIES, BERGEN, NORWAY
1980

FISKERIDIREKTORATETS SKRIFTER, SERIE HAVUNDERSØKELSER

[*FiskDir. Skr. Ser. HavUnders.*] [Report on Norwegian Fishery and Marine Investigations] is published at irregular intervals by the Directorate of Fisheries, Bergen, Norway. The journal is devoted to contributions on marine organisms or environments related to fisheries.

Original research articles or reviews in English are accepted, and manuscripts for publication should be adressed to:

The editor,
Fiskeridirektoratets Havforskningsinstitutt,
Postboks 1870–72,
N – 5011 Bergen–Nordnes,
Norway.

The general style of the journal follows *Style manual for biological journals* published by the American Institute of Biological Sciences, Washington D.C., USA.

Subscription and exchange office:

The library,
Fiskeridirektoratet,
Postboks 1870–72,
N – 5011 Bergen–Nordnes,
Norway.

Editor
ERLING BRATBERG

Fisk.Dir. Skr. Ser. HavUnders., *17*: 29–47

SOME BIOLOGICAL ASPECTS OF COD LARVAE (*GADUS MORHUA* L.)

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ABSTRACT

ELLERTSEN, B., MOKSNESS, E., SOLEMDAL, P., STRØMME, T., TILSETH, S., WESTGÅRD, T. and ØIESTAD, V. 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). *FiskDir. Skr. Ser. HavUnders.*, *17*: 29–47.

The development of functional larval stages is described in relation to different yolk sac stages. Morphological and histological work has been done concomitantly with the observation on the larval feeding behaviour. Larvae were fed different sizes of phytoplankters and nauplii of *Artemia salina*. Cod larvae proved to avoid small flaggelates but were active feeders on bigger sized phytoplankters. The problem concerning the influence of phytoplankters on the first feeding cod larvae is discussed. Cod larvae were shown to be a visual feeder on nauplii and the light intensity threshold was between 0.1–0.4 lux.

The point of no return (PNR) is tentatively determined, and the cod larval condition at that stage is compared to larval groups from the enclosure experiment (ELLERTSEN *et al.*, 1979b) which had experienced different feeding conditions. The following characters were found suitable for determining the condition of first feeding cod larvae: the size of the yolk sac, larval standard length, dry weight, height of the myotome, the differentiation of the swim bladder and the alimentary tract.

INTRODUCTION

The present paper describes some biological aspects of cod larvae, *Gadus morhua*, to support the interpretation of the condition of larvae sampled at sea. The main objective of the investigation has been to study and describe functional larval stages and the larval feeding behaviour on different plankters at the time of first feeding. Laboratory experiments have been performed under temperature condition close to the mean temperature in the main spawning area of the Arcto-Norwegian cod (see ELLERTSEN *et al.* 1979a).

Similar studies of the larval behaviour and feeding have been performed on other species (BLAXTER 1966, ROSENTHAL and HEMPEL 1970, HUNTER 1972). The cod larval growth and respiration are studied in the laboratory by LAURENCE (1978). The feeding behaviour and the ecology of marine fish larvae have recently been reviewed by HUNTER (1979). Extensive investigations on first feeding cod larvae are reported by ELLERTSEN *et al.* (1979a, b and c).

MATERIALS AND METHODS

Artificially fertilized eggs of Arcto-Norwegian cod were obtained in March from the Lofoten area. The eggs from various females were kept separate and were sent by air to the Institute of Marine Research, Bergen, the day after fertilization.

The eggs (10 ml) were incubated in 3 l perspex cylinders, with open circulation of filtered sea water. (TILSETH and STRØMME 1976). The cylinders were placed in temperature controlled water baths of 3°C and 5°C, ± 0.5°C. The salinity was from 34–34.7‰ during the experiment. About 500 larvae, hatched on the same day, were stocked in separate cylinders with the open circulation of filtered sea water.

DEVELOPMENT, LARVAL YOLK SAC STAGES

Ten larvae from each stock were conserved in 4% formalin every day and later examined for morphological studies and standard length measurement.

FEEDING INCIDENCE, INFLUENCED BY LIGHT INTENSITY

Feeding experiments were conducted in 3 l aquaria (15 cm in diam. 22 cm high) with stagnant filtered sea water. An «air lift» kept the density of food particles in the water volume homogeneous.

These experiments were designed to study the cod larval feeding behaviour and feeding incidence on different plankters of different sizes under different light conditions. Experiments were daily performed as feeding incidence on starved groups of 30 larvae from the same stock. Each experiment lasted for 6 hours; larvae were conserved in 4% formalin and later examined for the gut content.

Larvae were fed *Dunaliella* sp. (7–9 μm) at 1 000, 10 000 and 100 000 cells/ml. Fluorescent lamps provided about 1 000 lux at the water surface. The experiments started on day 1 and ended on day 12 after hatching. The dinoflagellat *Peridinium trochoidum* (50–80 μm) was given at food consentration of 1 000 cells/ml in three 3 l aquaria where the light intensity was

adjusted by neutral filters to 1 000, 10 and 0 lux at the water surface. The experiment started on day 5 and ended at the age of 12 days.

Cod larvae were fed *Artemia salina* nauplii (250 μm carapax length) at 1 nauplius/ml. Using neutral filters the light at the water surface was adjusted to 1 000, 10, 1.4, 0.4 and 0.1 lux. The experiment started on day 1 and ended on day 13 after hatching.

FEEDING BEHAVIOUR

Cod larvae were placed in a 10 x 10 x 1 cm wide perspex chamber in a thermostat at 5°C, and their feeding behaviour was observed through a low-powered binocular microscope.

BUOYANCY

Fourteen 250 ml glass cylinders containing sea water graded in 0.5‰ salinity steps from 28 to 34.5‰ were placed in a thermostat with a constant temperature of 5°C. Salinities were prepared by adding distilled water to sea water of 34.7‰ salinity. Thirty larvae were anaesthetized in 1 : 20 000 MS 222, and 10 larvae were transferred to each of three cylinders. In all instances larvae were rinsed in the same salinity as that of the experimental cylinder. The neutral buoyancy of larvae was assessed according to the method of SOLEMDAL (1971).

LARVAL RESPONSE TO LIGHT

Fifty larvae of the same spawn were transferred to a 130 cm high, 15 cm diameter perspex tube on the day of hatching. The tube was held in a temperature controlled perspex water bath at 5°C ± 0.5°C, placed in a lightproof observation chamber. The tube was illuminated from above by a 1 000 W halogen lamp. The light intensity could be varied by an adjustable auto transformer. A water bath was inserted between the lamp and the tube to prevent heating of the water. The light intensity was measured at the bottom of the tube.

The larval reaction to changes in light intensity was most easily observed following adaption to dark. Therefore larvae were adapted to 14 hours of dark. Then the light was slowly increased to 80 000 lux followed by a slow reduction to 1 000 lux, and the number of larvae moving vertically were observed 10 minutes later. The number of larvae showing swimming behaviour associated with searching for food were observed for 15 minutes following two hours adaption to light (1 000 lux). These observations were made daily from the time of hatching until death from starvation.

COD LARVAL CONDITION IN RELATION TO FIRST FEEDING

In an attempt to estimate the condition of first feeding cod larvae in relation to PNR, yolk sac larvae were released in the enclosure (see ELLERTSEN *et al.* 1979b) at the same time as larvae were starved in the laboratory.

In the present paper three groups of larvae will be compared. Two groups were released in the basin, referred to as «second group» and «third group». A batch of larvae from the third group starved in the laboratory at 6°C in two 8 liter jars. Each day larvae were sampled from the jars and the enclosure starting at the age of 4 days, and in this experiment ending at the age of 20 days. Larvae were preserved in 4% formalin and examined later for the following characters: the yolk sac stage was determined according to the description given on page 33 (see Fig. 1); standard length was measured to the nearest 0.1 mm; the myotome height was measured behind the anus to the nearest 0.01 mm; the larval dry weight was measured on a Beckmann electrobalance to the nearest 1 μg, and the development of the swim bladder and the gut was studied.

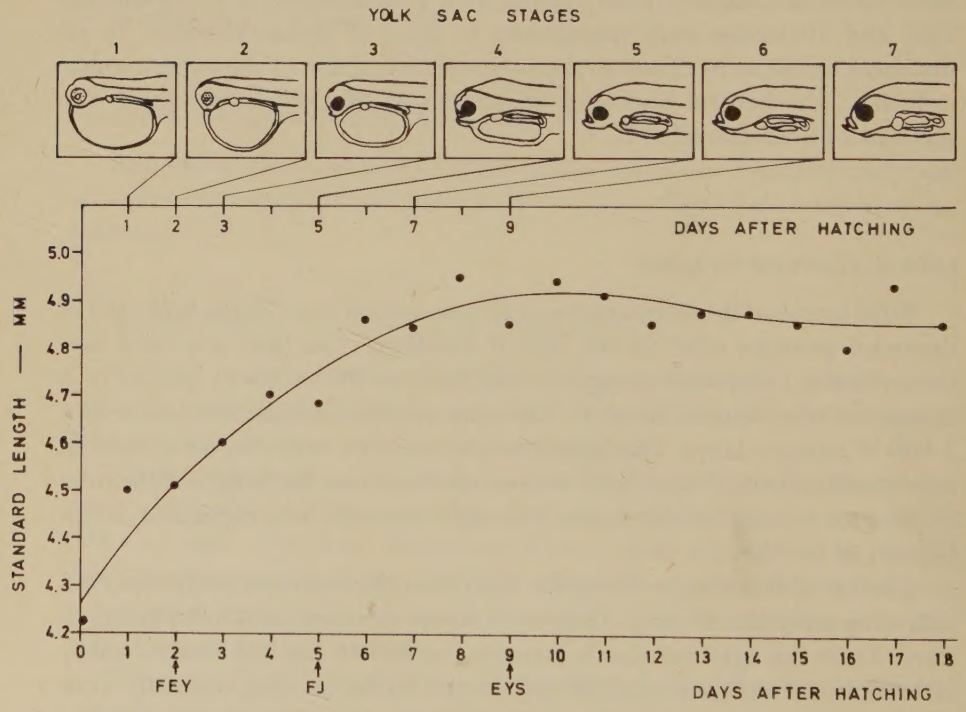

Fig. 1. Standard length of cod larvae from hatching until death from starvation at 3°C: points are the mean of ten larvae of the same female fish. The duration of characteristic yolk sac stages is plotted against larval age. The time of development of functional eyes (FEY), jaw (FJ) and the end of the yolk sac stage (EYS) are indicated.

RESULTS

DEVELOPMENT, LARVAL YOLK SAC STAGES

The development of the cod larval standard length at 3°C, and the following description of the yolk sac stages are shown in Fig. 1, from the time of hatching until death from starvation.

Stage 1: At the time of hatching the larvae were floating close to the surface with the yolk sac upwards. The mouth is not yet open, the eyes are not fully pigmented (greyish) and the yolk sac is eggshaped.

Stage 2: Within 24 hours the larvae get oriented and the yolk sac become spherical. The eyes become more pigmented (greyish-brown).

Stage 3: The mouth opens at the age of 2 days. The eyes are nearly fully pigmented, and more than 50 percent of larvae respond to a change in light intensity (Fig. 8). The yolk sac is elliptical.

Stage 4: At the age of 3 to 4 days the eyes become fully pigmented and the larval activity increases. The yolk sac is cylindrical.

Stage 5: At the age of 5 days the jaw becomes functional (Fig. 2), and larvae are for the first time observed with food particles in the gut. The yolk sac is still cylindrical. The gut has grown in volume and is bigger than the yolk sac.

Stage 6: Only remains of the yolk are observed in the yolk sac.

Stage 7: The yolk will be completely absorbed at the age of 9 days. The epithelium of the yolk sac and a few granules can be seen only. (Fig. 1.)

Incubation of larvae at 5°C will advance the development. The eyes will become functional at the age of 2 days and the jaw at the age of 4 days. The yolk sac will be fully absorbed within 8 days.

FIRST FEEDING AND FEEDING BEHAVIOUR

Cod larvae start first feeding on *Artemia* nauplii at the age of 5 days at 5°C. Observations of the larval feeding behaviour showed that the larva manoeuvred carefully towards the prey organism using the pelvic fins, opened the mouth, expanded the oral cavity and the nauplius was sucked into the mouth. It was observed that larvae chased and reacted to prey organisms in front, above and below them. If larvae missed prey organisms, they would follow the prey and make another try.

Histological examinations of the head and the jaw of the larva showed that the main morphological changes occurred from the day of hatching till the 5th day. During this period the Meckel's cartilages, quadratum and hyosymplecticum were fully formed and the jaw became functional (Arnfinnson, in press) (Fig. 2).

Starved larvae exhibited feeding behaviour until the day before mass mortality of the larval population which occurred at the age of 17 days at 5°C.

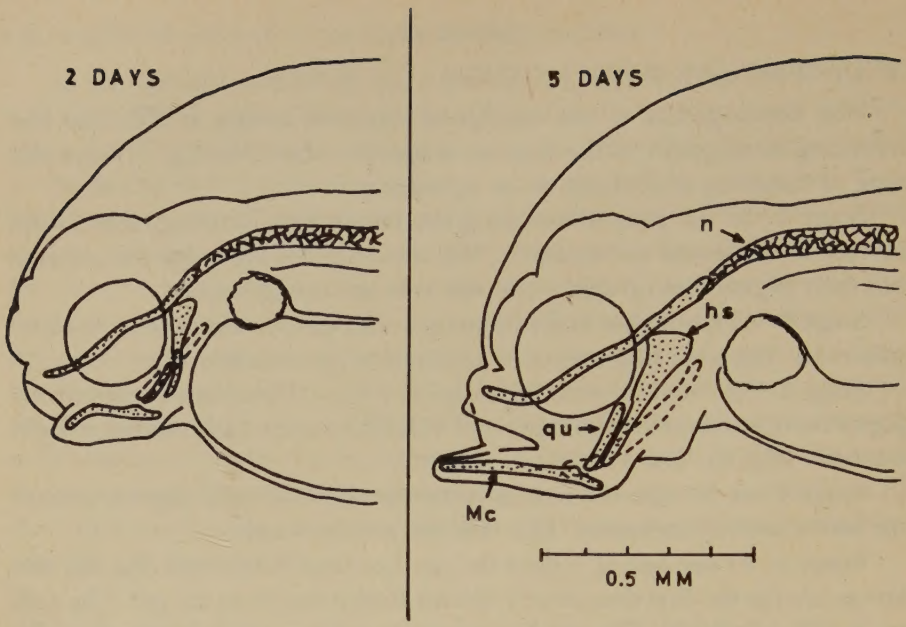

Fig. 2. Sections through cod larvae 2 and 5 days old. Mc: Meckel's cartilage, qu: quadratum, hs: hyosymplecticum and n: notochord.

FEEDING INCIDENCE, INFLUENCED BY LIGHT INTENSITY

The feeding incidence during 6 hour feeding sessions of cod larvae from the age of 1 day to the age of 13 days are shown in Fig. 3.

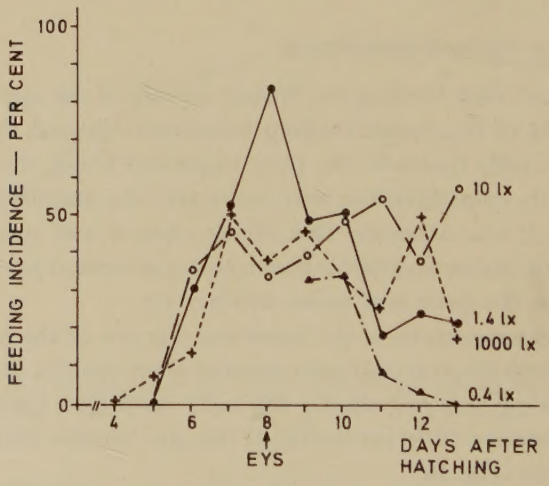

Fig. 3. Cod larval feeding incidence on *Artemia salina* nauplii at different light intensities following 6 hours feeding sessions. Larvae were starved 1, 2 .... 13 days respectively; points are the mean of 30 larvae of the same stock.

Cod larvae started feeding on *Artemia* nauplii on day 4. The feeding incidence increased towards the end of yolk absorption. The highest feeding incidence, 85%, was observed at 1.4 lux on the day of yolk exhaustion. Feeding incidence never exceeded 55% at light intensities of 10 and 1 000 lux. At these light regimes larvae were observed at the bottom of the cylinder at the end of the experiments. Feeding experiments at 0.4 lux started at the age of 9 days when feeding incidence was 33% and then dropped from 34% on day 10 to 0 on day 13. Cod larvae did not feed at 0.1 lux.

The cod larval feeding incidence during 6 hour feeding sessions on the flagellat *Peridinium trochoidum* (1 000 cells/ml) at 1 000, 10, and 0 lux is presented in Fig. 4.

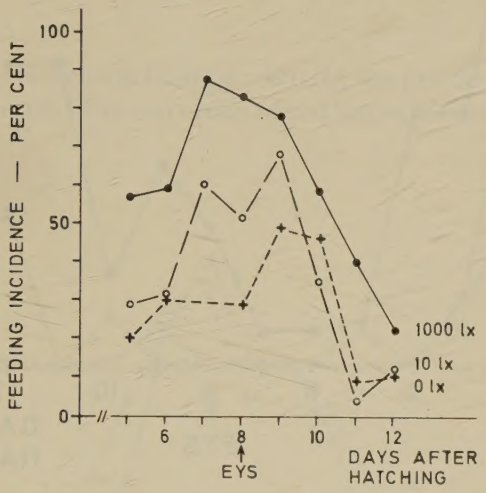

Fig. 4. Cod larval feeding incidence on *Peridinium trochoidum* at different light intensities following 6 hours feeding sessions. The larvae were starved 1, 2 . . . . 12 days respectively; points are the mean of 30 larvae of the same stock. Experiments started at the larval age of 5 days.

These experiments started at larval age of 5 days and terminated on day 12. The feeding incidence increased towards the end of yolk absorption and reached 90% on day 7 at 1 000 lux, and decreased at all three light regimes from the age of 9 to 12 days. The highest larval feeding incidence was observed at 1 000 lux. Cod larvae also proved to ingest *P. trochoidum* in complete darkness.

More than 80% of cod larvae were observed with *Dunaliella* sp. (100 000 cells/ml) present in the gut at the age of 1 day following 6 hour feeding experiment. Forty percent of larvae had «green guts» at the lowest flagellate density (1 000 cells/ml) (Fig. 5). An examination of live cod larvae, using a low-powered binocular microscope, showed that the flagellates incidentally

entered the mouth of larvae and covered the viceral arches. When the viceral arches were clogged, the flagellates were swallowed. A substantial reduction of larvae with «green guts» occurred from the fourth to the fifth day concomitantly with the development of the jaw which became functional. Microscopic observations of live larvae showed that they were able to spit out the flagellates whenever the viceral arches became clogged. An increase in number of larvae with green guts was observed at the end of the experiment.

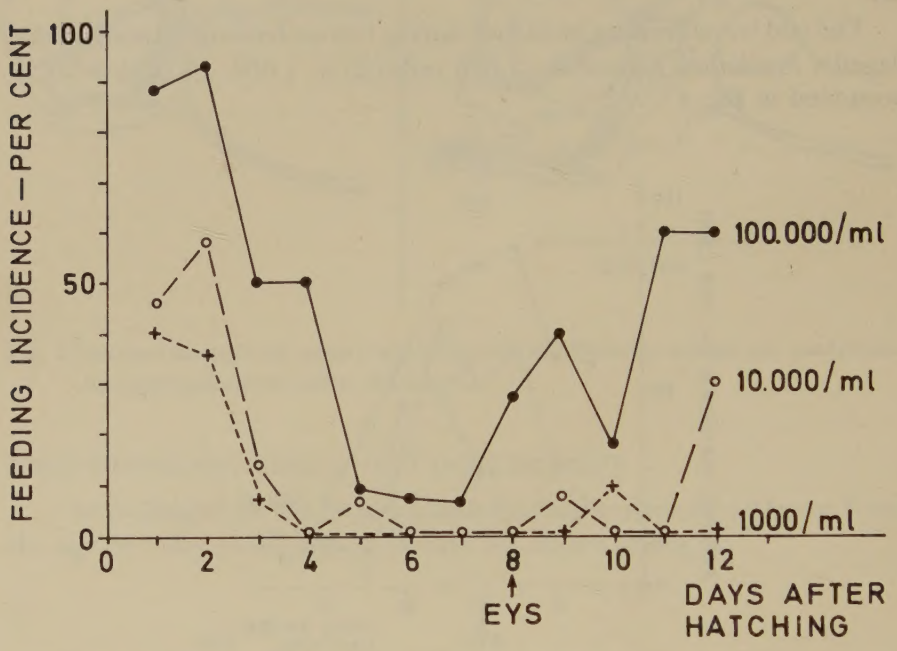

Fig. 5. Cod larval feeding incidence on *Dunaliella* sp. at different densities following 6 hours feeding sessions. Larvae were starved 1, 2 . . . . 12 days respectively; points are the mean of 30 larvae.

The relationship between the standard length of first feeding cod larvae (aged 6 to 12 days) and the mean number of food particles in the larval gut is presented in Fig. 6.

The figure shows the results from laboratory experiments. First feeding cod larvae were fed *Artemia* nauplii for 6 hours. These results are compared with the results from the enclosure experiment (larval age 7 to 10 days) and the investigation of first feeding cod larvae (yolk sac stage 5, 6 and 7), sampled at sea in the Lofoten (Fig. 6). All three investigations show that longer larvae are able to catch more nauplii than the shorter ones at first feeding (see also ELLERTSEN *et al.*, 1979 b, c).

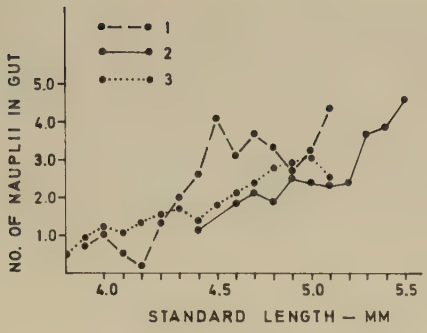

Fig. 6. The mean number of nauplii in the guts of first feeding cod larvae at different lengths observed; 1: in the enclosure experiment (n=290), 2: in the laboratory (n=123), and 3: larvae sampled in the Lofoten area (n=323). (See text and ELLERTSEN *et al.* 1979b, c).

BUOYANCY

The changes in neutral buoyancy during the period of yolk absorption till subsequent death from starvation of cod larvae of two females are shown in Fig. 7.

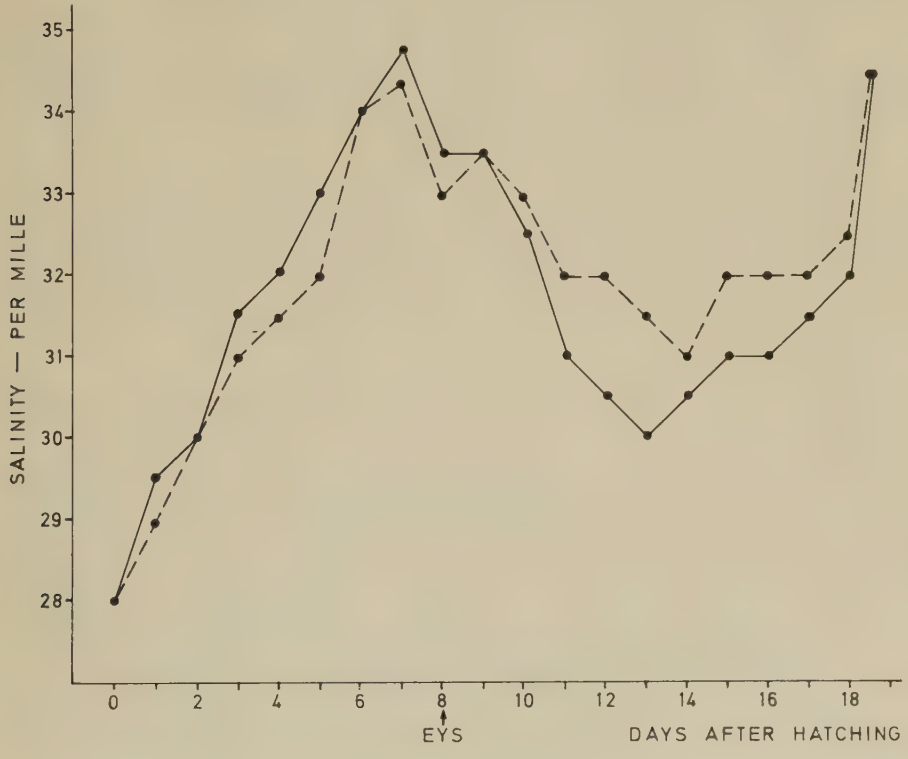

Fig. 7. Changes in neutral buoyancy in cod larvae of two female fish, from hatching until death from starvation; points are the mean of ten larvae.

Larvae were neutrally buoyant at about 28‰ salinity at the time of hatching and were heaviest at the end of the yolk exhaustion when they were neutrally buoyant at about 34.5‰ salinity. After the period of yolk absorption, the specific gravity decreased and reached a minimum on day 13–14 when larvae were neutrally buoyant at about 31–30‰ salinity. When larvae became moribund, the specific gravity increased, osmoregulation probably failed and they were sinking in 34.7‰ salinity.

LARVAL SWIMMING BEHAVIOUR, RESPONSE TO LIGHT

During the first 48 hours of larval life, cod larvae exhibited little locomotory activity. Two different swimming patterns were observed. A distinct feature of one of these patterns was that larvae executed a brief, but intense burst of swimming. The tail and body beat from side to side and the burst lasted for about one second. This pattern of swimming was dominant during the yolk sac period with an increasing burst frequency towards the end of yolk absorption. This pattern was very similar to the swimming pattern of anchovy larvae described as intermittent swimming by HUNTER (1972). After yolk exhaustion the larval activity dropped.

The second swimming pattern was a continuous swimming where larvae beat the tail continuously for several seconds. This reaction was strongly stimulated when tapping the wall of the tube, or whenever larvae collided with another larvae. This swimming pattern was obviously an escape or avoidance reaction.

Intermittent swimming was performed when larvae were making vertical movements in the tube as a response to the changes in light intensity or when they were searching for food. The burst frequencies, however, were about twice as high when larvae were moving vertically, 39.95 (SD = ± 4.63, n = 56) burst/min., as when swimming horizontally 20.10 (SD = ± 3.13, n = 78) burst/min.

The cod larval response to the change in light intensity is presented in Fig. 8.

When the light intensity was increased from 0 lux to 80,000 lux, and then slowly reduced to 1000 lux after 14 hours adaption to dark, larvae would initially be swimming up and down the tube. However, after a short period of time, larvae would swim downwards. The number of larvae responding to the change in light intensity was therefore recorded, following a period of 10 minutes. This observation was performed daily in order to test the larval activity and their ability to respond to the changes in light intensity.

At the time of hatching larvae did not respond to the increased light intensity. They floated more or less motionless close to the surface, even when the light was increased to above 80 000 lux. About 50% of larvae swam vertically down the tube at the age of 2 days as a response to the increased

light intensity. At the age of 3 days larvae exhibited swimming behaviour associated with feeding behaviour. On the fifth day more than 90% of the larvae responded to the changes in light and showed swimming behaviour associated with feeding behaviour. At the age of 9 to 10 days, the number of larvae performing these behaviour patterns decreased, and on the eleventh day the number of passive larvae increased. On the fourteenth day the first dead larvae were observed at the bottom of the tube; in the following three days all larvae were dead.

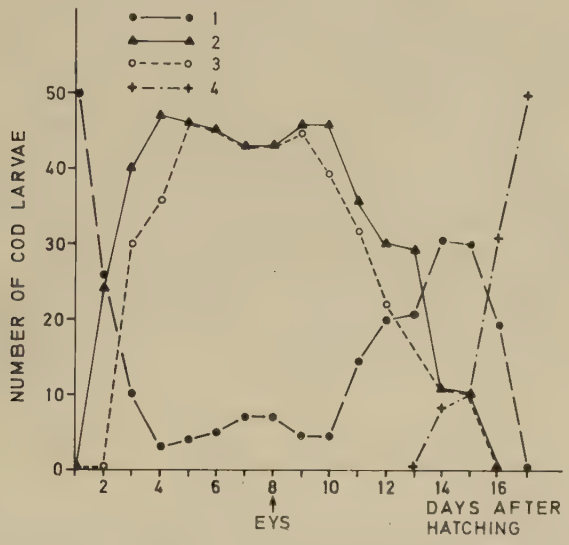

Fig. 8. Changes in the cod larval activity in relation to the larval age regarding the number of larvae floating passively close to the surface 1), responding to changes in light intensity 2), performing feeding behaviour 3) and the number of dead larvae observed at the bottom of the observation cylinder 4).

COD LARVAL CONDITION IN RELATION TO FIRST FEEDING

The changes in growth and development of the swim bladder and alimentary tract of two larval groups from the encolsure experiment are shown in Figs. 9 a, b, c and d. A group of larvae starved in the laboratory (Lab. group) consists of larvae of the same population as the «third group», see ELLERTSEN *et al.* (1979 b).

Larvae in the «third group» showed a very rapid growth in length, dry weight and myotome height compared to the lab. group and the «second group». However, initially the standard length of the «third group» was 5% shorter and the myotome height 7% higher compared to the laboratory reared group of the same age. This difference is probably an effect of shrinkage caused by the plankton net which killed larvae sampled in the enclosure before they were conserved in formalin. The «third group»

initiated feeding at the age of 5 days (yolk sac stage 5–6), and feeding incidence was observed close to 100% at the end of yolk exhaustion, i.e. on the 7th day (ELLERTSEN *et al.* 1979 b). More than 50% of larvae within the «third group» developed a transparent swim bladder at the age of 10 days.

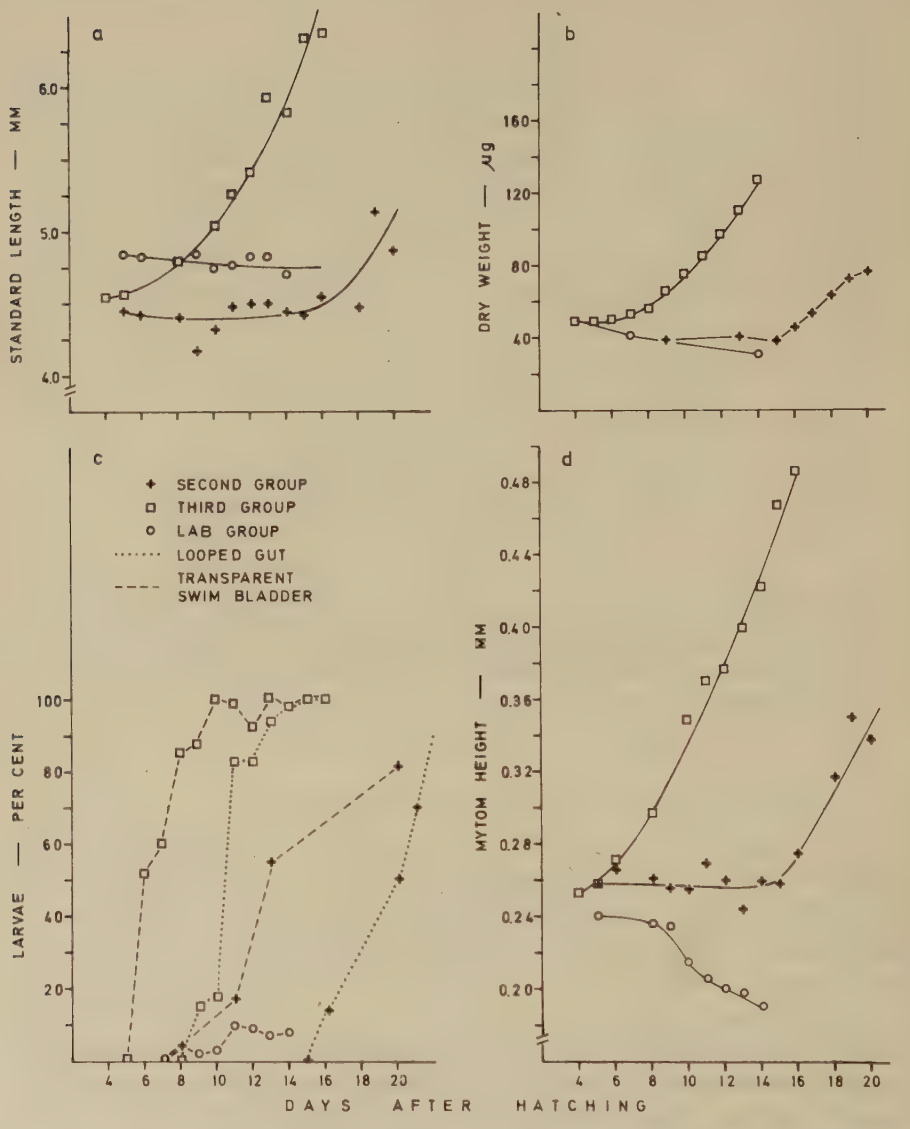

Fig. 9a, b, c and d. Changes in standard length, dry weight, the development of looped gut and swim bladder and myotome height in three groups of cod larvae under different feeding regimes in relation to larval age. (See text and ELLERTSEN *et al.* 1979b).

Only 10% of the lab. group ever developed a transparent swim bladder. The swim bladder was developed from opaque to transparent, and soon after it became filled with gas. Fifteen per cent of the «third group» were observed with a differentiated alimentary tract (looped gut) at the age of 9 days. The lab. group never differentiated the gut from a strait tube. Starved larvae reached a maximum standard length of 4.8 mm on the 9th day. The larval dry weight was reduced from about 50 μg at the time of hatching to about 30 μg on the day before mass mortality. The height of the myotome was reduced from 240 μm at the age of 6 days to 200 μm at the age of 12 days.

The «second group» was released into the basin when the feeding conditions were poor compared with the conditions under which the «third larval group» was released (Ellertsen *et al.* 1979 b). The «second group» was observed to initiate feeding at the age of 11 days, and the feeding incidence was observed close to 100% on the 14th day (Ellertsen *et al.* 1979 b); a delay of about one week compared with the «third group». The «second group» did not show any increase in growth before the 16th day. Larvae with transparent swim bladder were first observed on the 11th day; a delay of five days compared with the «third group». At the age of 16 days, larvae of the «second group» were first observed with a looped gut; a delay of seven days compared with larvae of the «third group».

DISCUSSION

The exact information about the development of the critical functional larval stages such as functional eyes, mouth, the locomotory patterns and the feeding behaviour is important when assessing the condition of larvae sampled at sea.

FEEDING BEHAVIOUR

Most fish larvae start feeding before the yolk is completely exhausted (Blaxter 1969). Cod larvae initiated feeding at yolk sac stage 5 (Fig. 1 and 3). This event coincided with the development of a functional jaw (Fig. 2) which occurred 2 to 4 days before the yolk exhaustion, depending on the temperature.

The cod larval feeding behaviour was very similar to the biting attack of adult fish. Cod larvae do not assume a sinuous body posture before striking at the prey as described for herring larvae, *Clupea harengus* (Rosenthal and Hempel 1970), anchovy larvae (Hunter 1972) and plaice larvae (Riley 1966). They attack the prey in a similar way as mackerel larvae, *Scomber japonicus* (Hunter and Sanchez MS), which make a posterior drive with the tail and with open mouth when capturing the prey. Cod larvae were observed to suddenly expand the oral cavity and suck the prey into the mouth.

The feeding success was very difficult to evaluate because in many instances the feeding behaviour was observed only with the aid of a low-powered binocular microscope. However, the feeding success at first feeding is thought to be high because larvae perceive and chase the prey in front, above and below the level of the body axis. Cod larvae also make another try if missing the prey. Cod larvae were also able to swim backwards. This great manoeuvring ability was also observed in plaice larvae which had a very high feeding success, i.e. 32–62% at the onset of feeding (Blaxter and Staines 1971), in contrast to the less manoeuvrable herring larvae which had a very low feeding success, 2–6% at the onset of feeding (Blaxter and Staines 1971).

LIGHT INTENSITY THRESHOLD

Most marine fish larvae are visual feeders, and the feeding occurs only above a certain light intensity (see Blaxter 1966). Cod larvae were able to capture *Artemia* nauplii at 0.4 lux, but not at 0.1 lux. This value was close to the light intensity threshold observed in herring larvae (Blaxter 1966). An increase in the feeding incidence, observed at the onset of feeding in cod larvae till yolk exhaustion, was probably due to an increase in the activity, indicated in Fig. 8. The highest feeding incidence, about 85%, was observed at 1.4 lux. The feeding incidence never exceeded 55% at 10 and 1000 lux. The light intensity at 1.4 lux could be close to the optimum light condition when cod larvae are feeding on *Artemia* nauplii, while the lower feeding incidence at 10 and 1000 lux could be due to an induced negative phototaxis. This was probably the case at the highest light intensity since at the end of the experiment the majority of larvae were observed at the bottom of the experimental cylinder. However, when feeding on smaller particles (*Peridinium trochoidum*, Fig. 4) the highest feeding incidence was observed at 1000 lux, probably due to smaller particles which are more visible at the higher light intensity. Cod larvae were also observed with *P. trochoidum* present in the gut in complete darkness. This was probably due to the high particle density (1000 cells/ml) and not to active feeding.

The light intensity threshold for visual feeding of cod larvae on nauplii is probably close to 0.1 lux. This value will determine the hours available for feeding of cod larvae at a certain latitude and time of year. According to the figure presented by Blaxter (1966 Fig. 3), there are 22–24 hours available for feeding of cod larvae in May in the Lofoten area. Examinations of the gut content of cod larvae sampled at 24 hours stations in the Lofoten area revealed the newly eaten nauplii at all hours (Ellertsen *et al.* 1979 c). At the Flødevigen station (Southern Norway), the time available for feeding of cod larvae was estimated to 16 hours in April. The results from the enclosure experiments from the 24 hour stations showed that newly eaten nauplii

were found only in the gut of cod larvae during daytime and coincided fairly well with the estimated period (Ellertsen *et al.* 1979 b).

COD LARVAL FEEDING IN RELATION TO PHYTOPLANKTERS

Fish larvae have been frequently reported with green food remains in the gut (Lebour 1919). Wiborg (1948) reports the same findings in cod larvae from the Lofoten area. Nordeng and Bratland (1971) have identified the phytoplankters *Peridinium pellucidum* and *Coscinodiscus* sp. in the gut of cod larvae from the same area. The cod larval feeding behaviour on the phytoplankters *Dunaliella* sp. and *P. trochoidum* were studied in our laboratory.

The smallest particles (*Dunaliella* sp.) were not actively fed upon. This was also the case when anchovy larvae were given *Dunaliella* sp. (Scura and Jerde 1977). The flagellates entered the unmovable mouth of young cod larvae by accident. The cells clogged the viceral arches, and clusters of flagellates were swallowed. Larvae were able to spit out the particles when the jaw became functional. This was clearly demonstrated by the substantial reduction in the number of larvae with «green gut» following 6 hour feeding sessions during which *Dunaliella* sp. were given in surplus to 5 days old larvae (Fig. 5). An increase in the number of larvae with *Dunaliella* sp. present in the gut at the end of the experiment is probably due to starved and enfeebled larvae. This effect was clearly seen when larvae were starved beyond the PNR, and then in surplus fed *Dunaliella* sp. (Fig. 5).

Single cells of small flagellates are only visible using a microscope with high magnifications. The cells were observed in the larval gut as clusters and appeared under a low-powered binocular microscope as green food remains. There is a possibility that the reported observations on cod larvae with green guts could have been cod larvae with an unfunctional jaw or older enfeebled larvae which has passed the PNR. These larvae might have been exposed to high densities of small flagellates. A density of 1000 cells/ml is frequently observed in the northern Norwegian coastal waters during the spring phytoplankton bloom (Schei 1974).

Cod larvae proved to be active feeders on bigger phytoplankters. When given *P. trochoidum* as the only food, the feeding incidence of larvae increased from yolk sac stage 5 to yolk absorption, stage 7. The cod larval feeding incidence on *P. trochoidum* was substantially reduced at the PNR (Fig. 4) in contrast to the feeding incidence when given *Dunaliella*. Cod larvae would actively feed on *P. trochoidum* even at moderate densities (50 cells/ml, see Ellertsen *et al.* 1976). However, larvae would be selective concerning the size and would elect bigger particles than 100 μm if those were present at the same time as P. *trochoidum* (Ellertsen *et al.* 1979 b, c).

Unidentified green food remains in the gut of cod larvae could also be copepod fecal pellets. Some of these pellets are of a suitable size for being

elected by cod larvae. Single phytoplankton cells in the pellet are difficult to identify, but when the pellet is newly eaten, the pellet itself can be easily recognized. This was observed in the bioassay experiment described by Ellertsen *et al.* (1979 c).

The nutritional value of phytoplankters for fish larvae is uncertain. However, Lasker *et al.* (1970) have successfully reared first feeding anchovy larvae on the dinoflagellate *Gymnodinium splendens.* Lasker (1975) also demonstrated the significance of *G. splendens* in adequate density at the onset of feeding of the Northern anchovy larvae along the Californian coast. Most fish larvae feed on all species of dinoflagellates. Anchovy larvae prey heavily upon *P. trochoidum* (Scura and Jerde 1977). However, Scura and Jerde (1977) made laboratory experiments and demonstrated that only unarmored dinoflagellates were digested by anchovy larvae. Investigations of the gut content of cod larvae following a 6 hour feeding session on *P. trochoidum* did not show any decoloration of the flagellates. Rearing of cod larvae on *P. trochoidum* was unsuccessful. These observations indicate a minor or no importance of the phytoplankters as a food organism for first feeding cod larvae. Bioassay experiments using wild plankton showed that the first feeding cod larvae were able to digest nauplii completely within 5 hours (Ellertsen *et al.* 1979 c).

POINT OF NO RETURN

The cod larval PNR was determined according to the method of Blaxter and Ehrlich (1974), based upon the change in the larval activity and buoyancy. The change in the cod larval buoyancy (Fig. 7) followed the same pattern as described for plaice larvae by Blaxter and Ehrlich (1974), with a steady decrease in buoyancy from hatching to yolk exhaustion. From this stage on the buoyancy was increased, probably due to a decrease in protein and an increase in water content as the larvae were starving. From the 14th day on, the buoyancy decreased again, probably caused by osmoregulation which was gradually failing. Blaxter and Ehrlich (1974) found a correspondence in the change of buoyancy and activity as larvae were starved and became moribund. The same pattern was found in cod larvae (Figs. 7 and 8). The day 11 is assumed to be critical (at 5°C) if larvae do not get food. A percentage of larvae exhibiting swimming behaviour associated with feeding behaviour was reduced from 64% on the 11th day to 44% on the 12th day (Fig. 8). This observation corresponds reasonably well with the 50% reduction in the feeding ability of cod larvae, described by Laurence (1978).

The cod larval feeding ability obviously depends on temperature, the size and density of food particles and light condition. An intraspecific variation has to be considered as well. This aspect needs further investigation.

There is obviously an advantage to start exogenous feeding before yolk exhaustion and thereby obtain an additional energy supply. This is clearly demonstrated in Fig. 9 a, b, c and d which show a dramatic difference in growth and morphological development when comparing the two larval groups.

Longer larvae were also observed to be able to catch more prey organisms than the shorter ones (Fig. 6). This is probably due to the increased searching abilities with growth since speed, capture success and perceptive distance are functions of length or age (HUNTER 1979). Larvae that start feeding before the yolk exhaustion will also have an increased dry weight and myotome height compared with starved larvae at yolk absorption (Fig. 9, b, d).

Even more important, cod larvae proved to differentiate the swim bladder and gut at a very early larval stage when achieving a surplus of energy before yolk exhaustion (Fig. 9 b). These observations can be utilized when assessing the condition of cod larvae caught at sea. Previous laboratory work indicates that starvation can be identified by chemical and histological criteria (EHRLICH 1974, O'CONNEL 1976) as well as by morphometric methods (SHELBOURNE 1957, BLAXTER 1971). A morphometric technique and morphological development characters are preferable because they can be applied routinely. As a result of our investigations we recommend the following six characters in assessing the condition of cod larvae; (1) the yolk sac stage, (2) larval standard length, (3) myotome height, (4) dry weight and the state of differentiation of (5) the swim bladder and (6) alimentary tract. Cod larvae at yolk sac stage 7 with a transparent swim bladder, looped gut, standard length $\geqq$ 5.0 mm, dry weight $\geqq$ 50 μg and myotome height $\geqq$ 250 μm have experienced good feeding conditions. Cod larvae at the same yolk sac stage without differentiated swim bladder and gut, and with morphometric values lower than the ones described above might have experienced less favourable feeding conditions at first feeding. Cod larvae at yolk sac stage 7, standard length $\leqq$ 5.0 mm, dry weight $\leqq$ 40 μg and myotome height $\leqq$ 220 μm without a differentiated alimentary tract and swim bladder would be in a critical starving condition and possibly close to the PNR. These characters have been applied for identifying cod larval runts in the enclosure experiment (see ELLERTSEN *et al.* 1979 b). Further investigations have been undertaken in order to determine the importance of each of these characteristics, and to find a simple routine for the assessment of the cod larval condition at sea.

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Received 15 October 1979
Printed 2 June 1980

FiskDir. Skr. Ser. HavUnders., *17*: 49–70.

ANGULAR MEASURES OF DORSAL ASPECT TARGET STRENGTH FUNCTIONS OF FISH

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ABSTRACT

FOOTE, K. G. 1980. Angular measures of dorsal aspect target strength functions of fish. *FiskDir Skr. Ser. HavUnders.*, *17*: 49–70.

Three angular measures of dorsal aspect target strength functions in the pitch plane are computed for previously gathered acoustic data on three gadoid fishes, two clupeoid fishes, and mackerel. These measures are the angle of maximum dorsal aspect backscattering cross section, the central angle of the backscattering cross section, and the dispersion of the cross section about the central angle. Each measure is regressed linearly on fish length. The statistical significances of the estimated regression coefficients are computed. Systematic differences are attributed to fish anatomy: backscattering cross sections of the considered swim bladder-bearing fishes are concentrated about negative tilt angles of several degree magnitude, which is attributed to the inclination of the swim bladder axis. Backscattering cross sections of mackerel, which lacks a swim bladder, are approximately balanced about the horizontal.

INTRODUCTION

The general complexity of the orientation dependence of fish target strength functions or backscattering cross sections at ultrasonic frequencies is well known, cf. references in FOOTE (1979a). For purposes of interpreting the results of echo integration (FORBES and NAKKEN 1972), rather simple relationships of target strength and fish length have been derived. Two methods of determining this relationship have employed regression analysis. In one method the dependent regression variable is a logarithmic measure of a special value of the backscattering cross section, e.g., maximum dorsal aspect value (MIDTTUN and HOFF 1962, YUDANOV *et al.* 1966, NAKKEN and OLSEN 1977), maximum near dorsal aspect value (MCCARTNEY and STUBBS 1971), and maximum side aspect value (LOVE 1969). In the other method the dependent variable is the same logarithmic measure of the average of the backscattering cross section with respect to the geometric, acoustic, and behavioural circumstances of observation (FOOTE 1978, 1979a–c, 1980a). In either case, if only through use of regression analysis to condense large quantities of data to manageable proportions, as in the derivation of simple target strength-to-length relationships, much scattering information is lost.

Some examples of other systematic scattering dependences of interest in

acoustic studies of fish stocks, which aim directly or indirectly to improve abundance estimates, are mentioned: The probability density function of observed effective scattering strength of fish may facilitate classification (FOOTE 1979d), as may statistical moments of echo energy from aggregations (FOOTE 1980b). The effective acoustic sampling volume depends on the detailed scattering properties of fish (FOOTE 1979e), which is of significance to the echo-counting method of assessing fish abundance (FORBES and NAKKEN 1972). Correction of echo integrator or echo counter estimates of fish abundance derived from use of sector scanning sonars in the vertical plane, as in avoidance reaction studies, similarly depends on the backscattering cross sections of fish (FOOTE 1979e).

Several additional examples of systematic target strength dependences, which are also of use in avoidance reaction studies (OLSEN 1979), are considered in this paper. These are measures of the angular characteristics of the dorsal aspect target strength function in the pitch plane. Three quantities are considered: the angle of maximum backscattering cross section, the angle of mean concentration of backscattering cross section, and the dispersion of the backscattering cross section about this central angle. The length dependences of the several angular measures are derived in this study for three gadoid species, two clupeoid species, and mackerel, for which measurements of the dorsal aspect target strength functions at 38 and 120 kHz exist (NAKKEN and OLSEN 1977, FOOTE and NAKKEN 1978). The statistical significances of various systematic length dependences and means of the angular measures are discussed.

MATERIALS AND METHODS

The source data for the computations of this study are the tabulated measurements of NAKKEN and OLSEN (1977) of the dorsal aspect target strength functions of six fishes at two ultrasonic frequencies (FOOTE and NAKKEN 1978). The number and represented length ranges of the measured functions for each species and frequency are presented in Table 1.

Table 1. Numbers and applicable length ranges of measured dorsal aspect target strength functions under analysis.

Fish	Data at 38 kHz		Data at 120 kHz	
	Number	Length range (cm)	Number	Length range (cm)
Cod *(Gadus morhua)*	68	6.7–96.0	44	6.7–67.0
Saithe *(Pollachius virens)*	59	9.1–68.0	48	9.1–68.0
Pollack *(Pollachius pollachius)*	44	19.7–61.0	39	19.7–52.0
Herring *(Clupea harengus)*	25	10.0–32.4	30	8.7–32.4
Sprat *(Sprattus sprattus)*	21	6.6–17.6	24	6.6–17.6
Mackerel *(Scomber scombrus)*	35	29.7–41.5	24	29.7–41.5

A characteristic measure of the dorsally sensed backscattering cross section is the pitch or tilt angle of maximum backscattering cross section. This is defined here for a particular backscattering cross section function σ of tilt angle θ by the following prescription:

$$\sigma(\alpha_o) = \text{Max } \{\sigma(\theta) \text{ for all } \theta\}, \tag{1}$$

where α_o is the sought angle of maximum backscattering cross section in the pitch plane.

The central tilt angle of backscattering cross section is defined by the expression

$$\alpha_1 = a^{-1} \int_{-\pi/4}^{\pi/4} \theta \, \sigma(\theta) \, d\theta, \tag{2}$$

where a is the normalization factor,

$$a = \int_{-\pi/4}^{\pi/4} \sigma(\theta) \, d\theta. \tag{3}$$

This makes the likely assumption that, for the approximately fusiform fish of consideration, the backscattering cross section function is concentrated in the dorsal region of the pitch plane.

A measure of the dispersion in backscattering cross section about the central angle is the second central moment of backscattering cross section,

$$\alpha_2^2 = a^{-1} \int_{-\pi/4}^{\pi/4} (\theta - \alpha_1)^2 \, \sigma(\theta) \, d\theta. \tag{4}$$

The same assumption of approximate concentration of backscattering cross section in the dorsal region is also invoked here in the delimitation of the integration range.

Because the measurements of the dorsal aspect target strength functions were made at one-degree intervals over the 90-degree range in tilt angles from –45 to +45 deg, the integrals of Eqs. 2–4 are approximated by finite summations. Extraction of the angle of maximum dorsal aspect backscattering cross section, as in Eq. 1, is similarly approximate. In all computations the length-to-wavelength ratio is confined to the approximate range of 2 to 80, which makes plausible the excellence of the several approximations.

The several computed angular measures are regressed linearly on fish length for similarly analyzed scattering data of homogeneous species and frequency content according to the linear expression

$$\alpha = b_o + b_1 \, l,$$

where α is a given characteristic angular measure expressed in degrees and l is the fish length in centimetres. Estimates of the regression coefficients b_0 and b_1, which are denoted by the respective circumflexed symbols $\hat{b}_0$ and $\hat{b}_1$, are computed in accordance with the least squares criterion (WILKS 1962). The corresponding standard errors of coefficients are computed.

The significances of the estimated coefficients are obtained from the t-statistic

$$t_b = \hat{b} \,/\, est[SE(\hat{b})],$$

where $est[SE(\hat{b})]$ is the estimated standard error of regression coefficient estimate $\hat{b}$. The number of degrees of freedom of the statistic, whether for b_0 or b_1, is $N-2$, where N is the number of independent data in each set. This number is specified in Table 1. Significance levels corresponding to the t-statistics are also tabulated. The meaning of an arbitrary significance level γ, for example, is the following:

$$Prob(b \neq 0) = 1 - \gamma,$$

that is, the probability that the estimated regression coefficient b is non-vanishing is $1-\gamma$. Thus the probability of wrongly rejecting the hypothesis that the regression coefficient essentially vanishes is $1-\gamma$. Small values of γ therefore indicate likely non-vanishing values of the estimated regression coefficient.

A similar statistical analysis is carried out for the means of the several angular measures.

RESULTS

Computations of the three angular measures of dorsal aspect target strength functions are presented in Figs. 1–12. Each figure consists in a set of three scatter diagrams of the several angular measures on fish length. The corresponding least squares linear regressions are shown. Statistical analyses of these regressions and of the mean angular measures are presented in Tables 2–4, which are discriminated by type of angular measure.

DISCUSSION

The main characteristics of the angle measure data presented in Figs. 1–12 are the lack of a trend in the maximum and central angles of the backscattering cross section, but general negativity of the same measures in the mean, and a slight upwards trend of the dispersion angle with increasing fish length. These observations are confirmed by inspection of Tables 2–4.

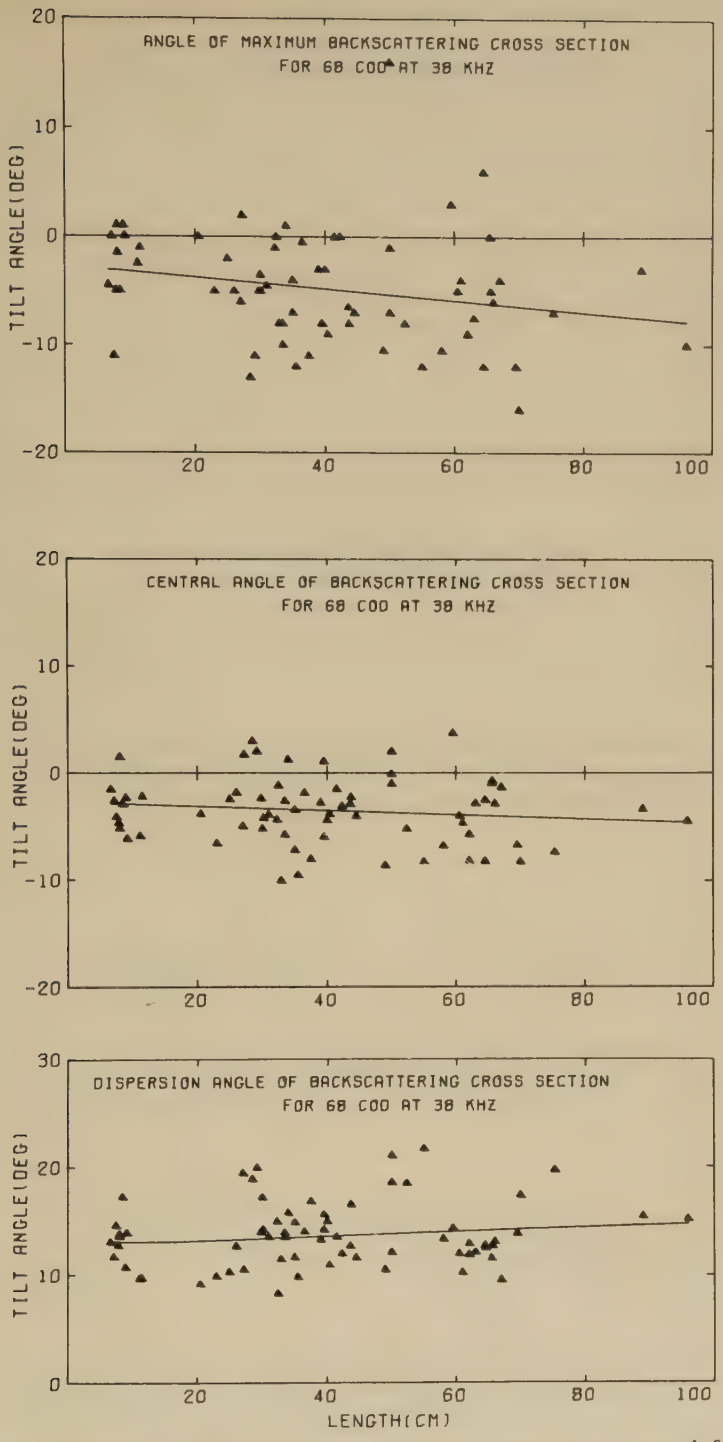

Fig. 1. Characteristic angular measures of measured dorsal aspect target strength functions of 68 cod at 38 kHz.

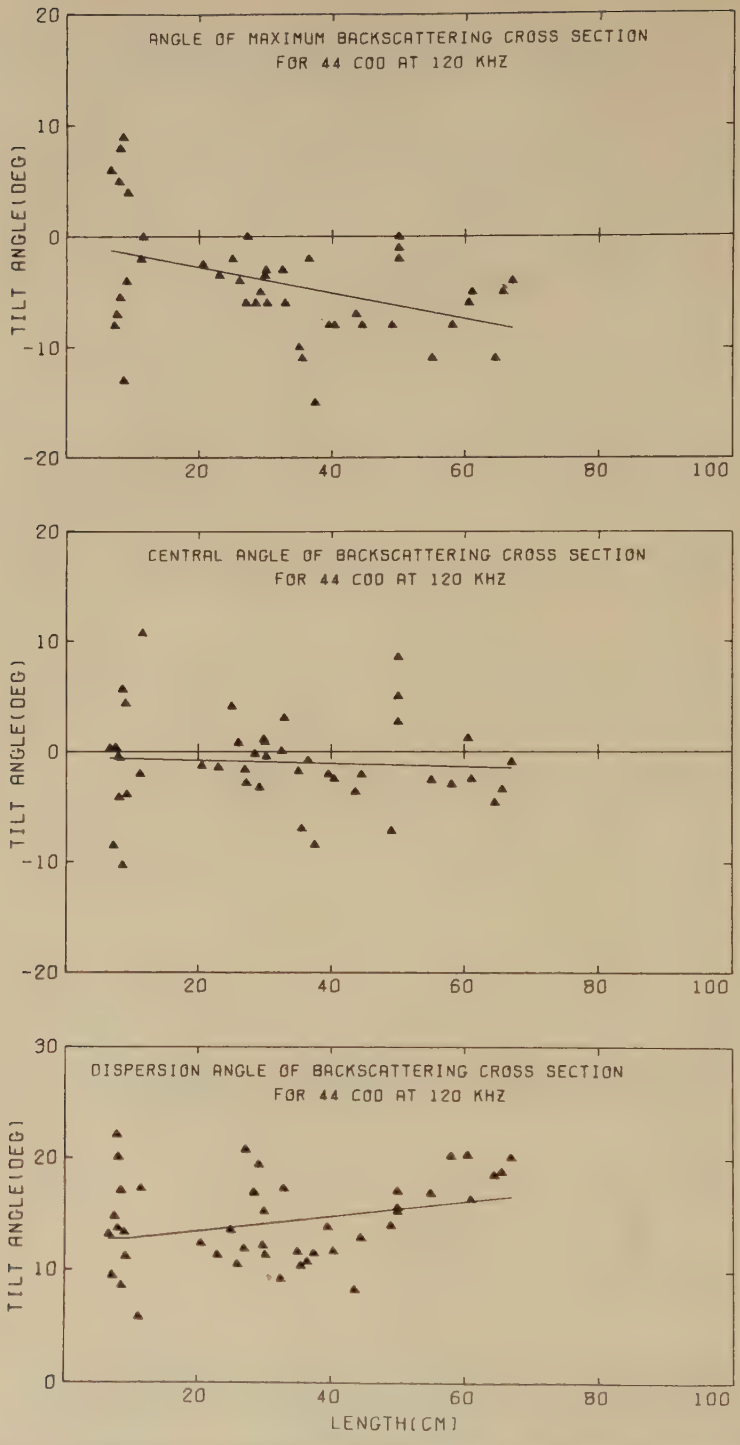

Fig. 2. Characteristic angular measures of measured dorsal aspect target strength functions of 44 cod at 120 kHz.

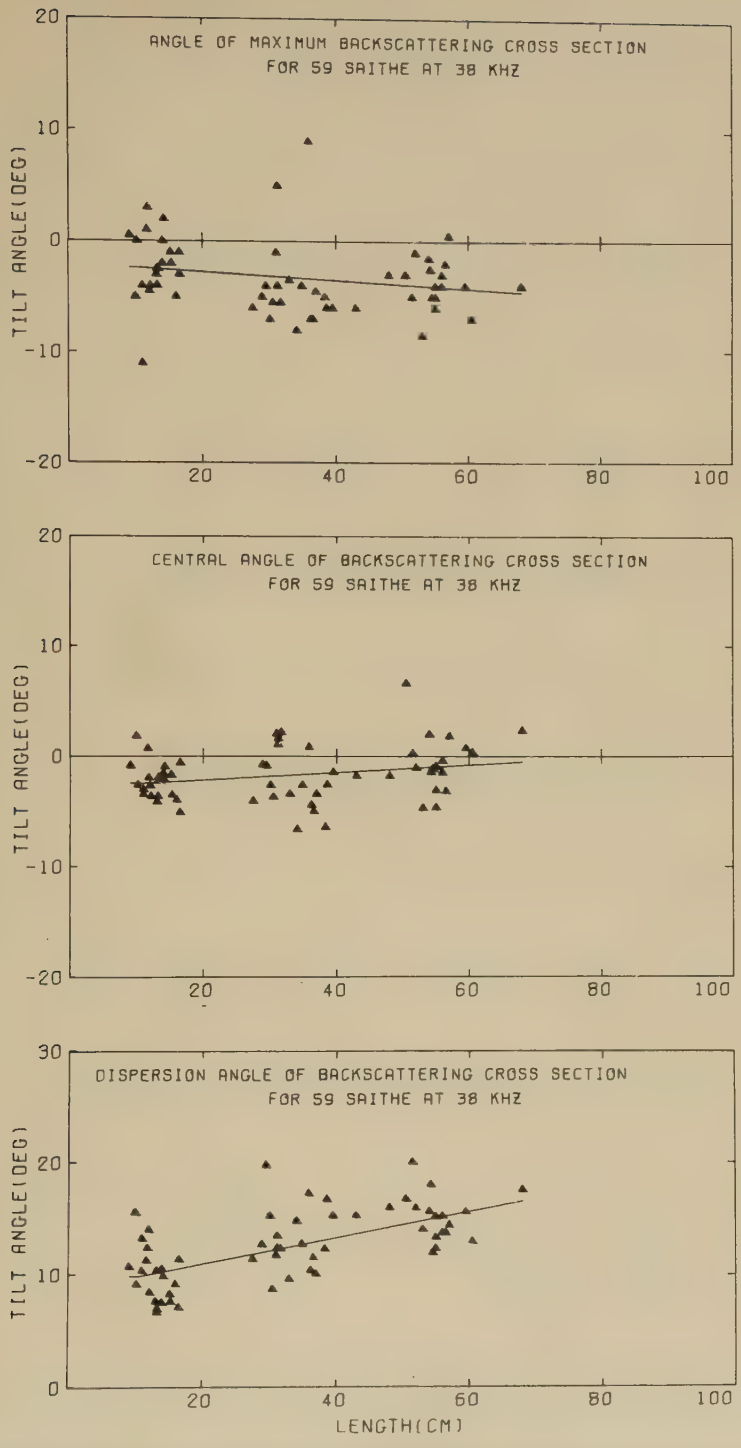

Fig. 3. Characteristic angular measures of measured dorsal aspect target strength functions of 59 saithe at 38 kHz.

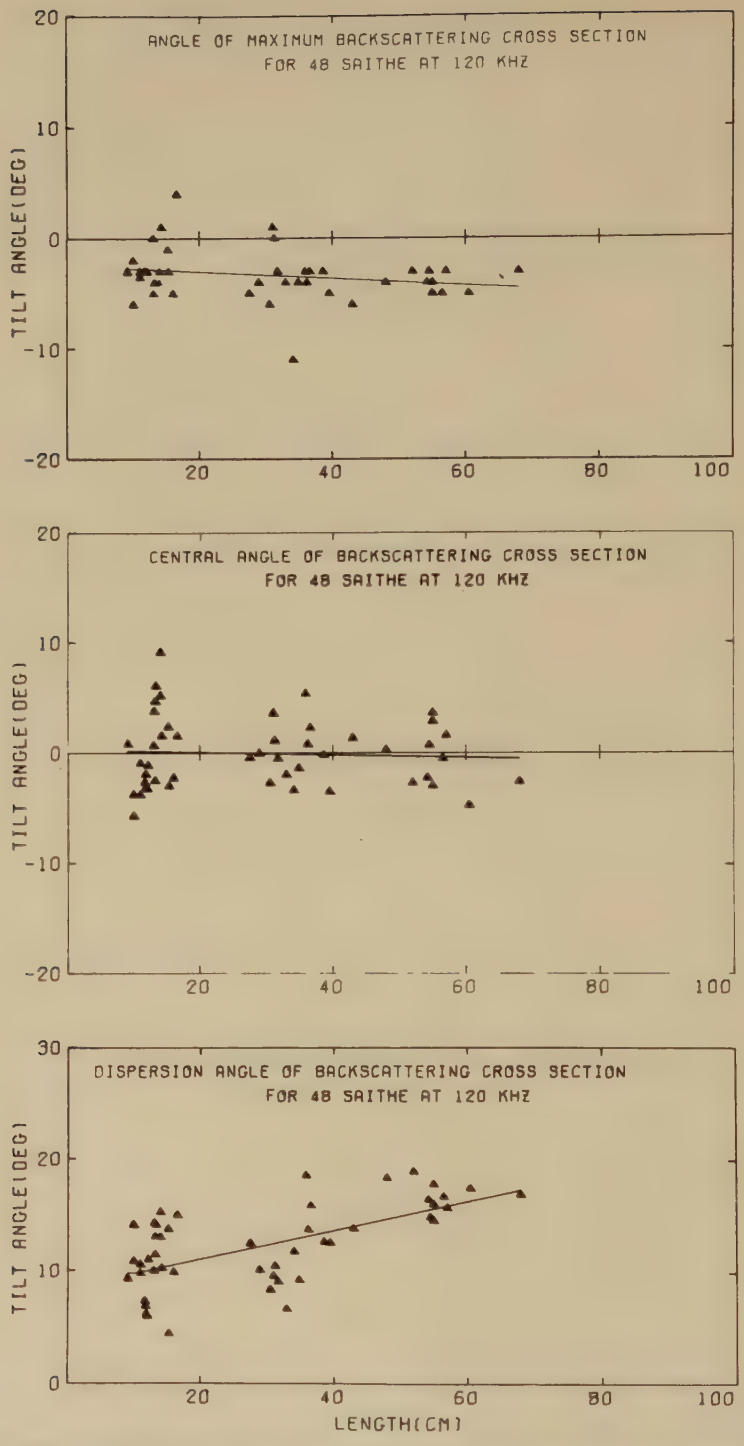

Fig. 4. Characteristic angular measures of measured dorsal aspect target strength functions of 48 saithe at 120 kHz.

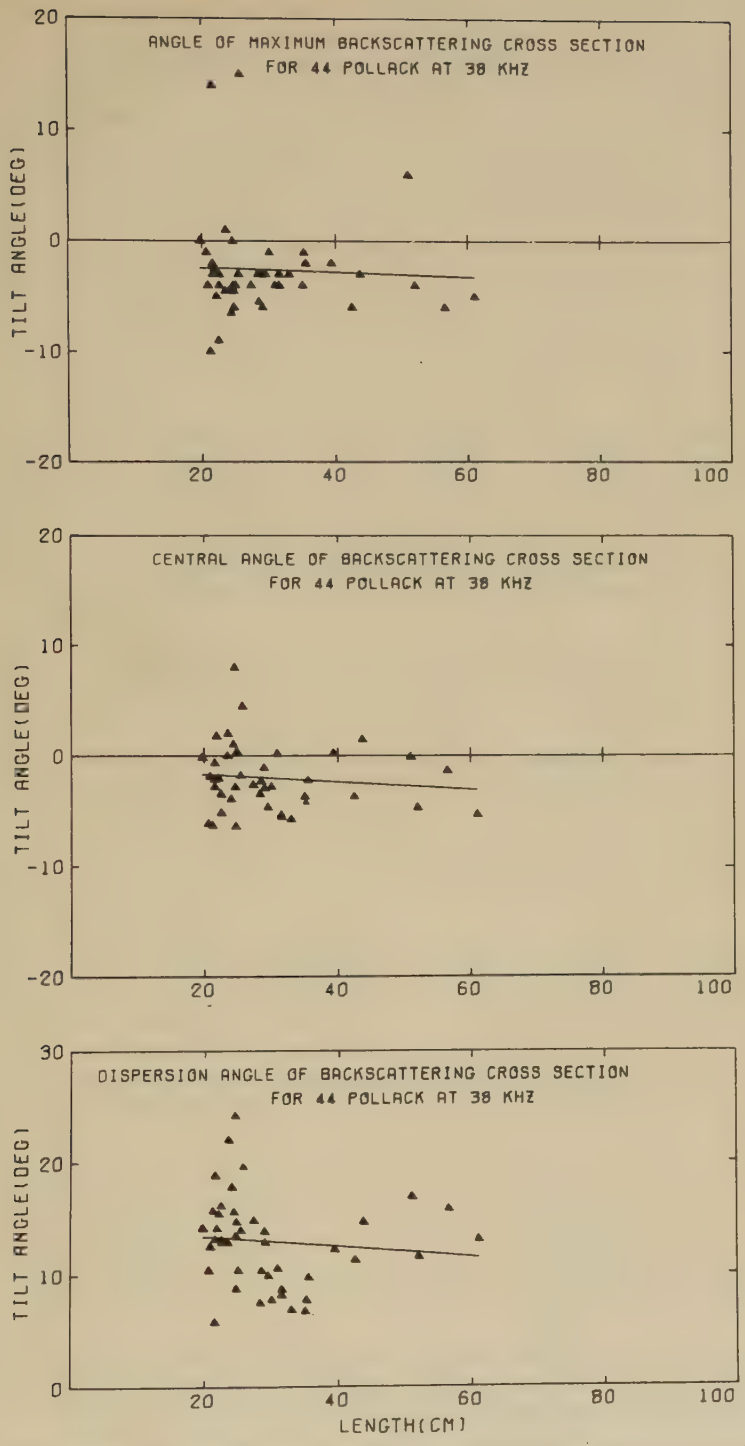

Fig. 5. Characteristic angular measures of measured dorsal aspect target strength functions of 44 pollack at 38 kHz.

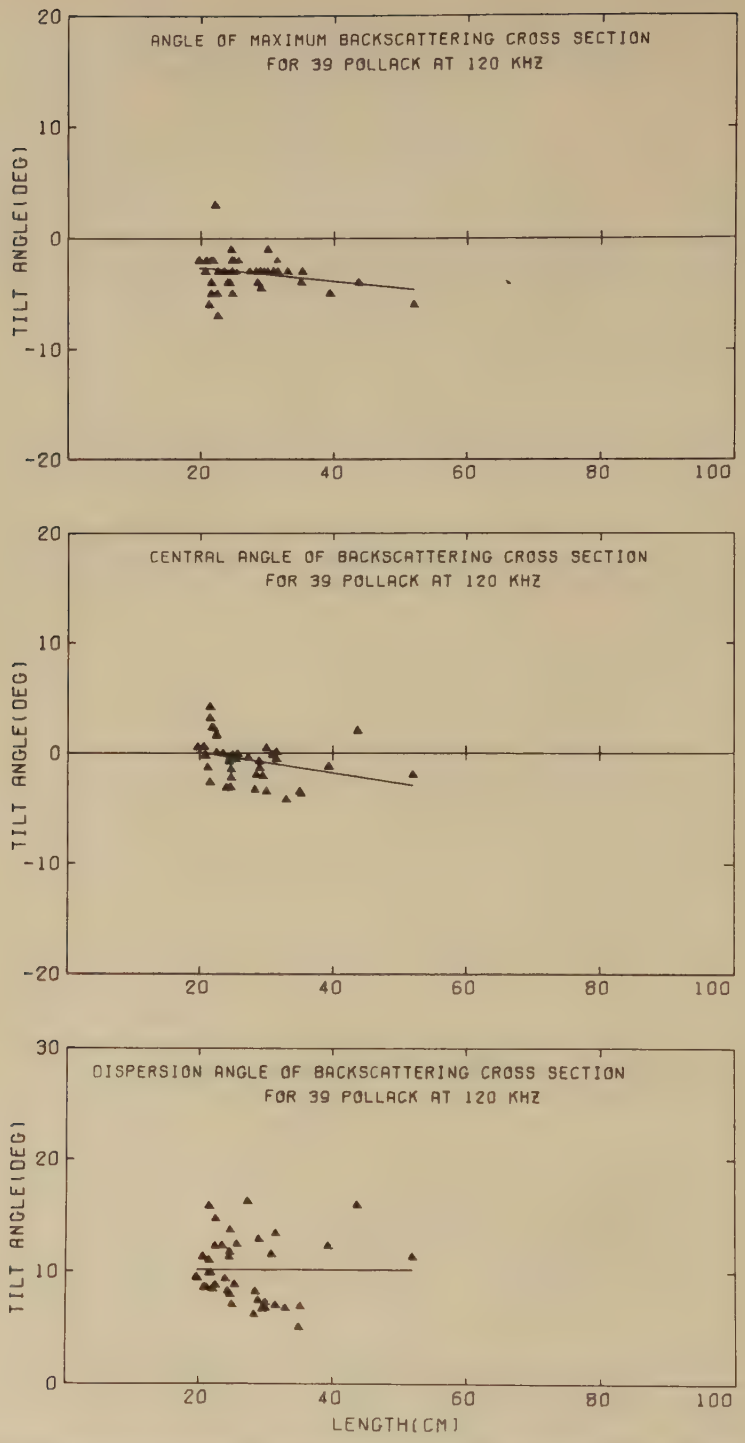

Fig. 6. Characteristic angular measures of measured dorsal aspect target strength functions of 39 pollack at 120 kHz.

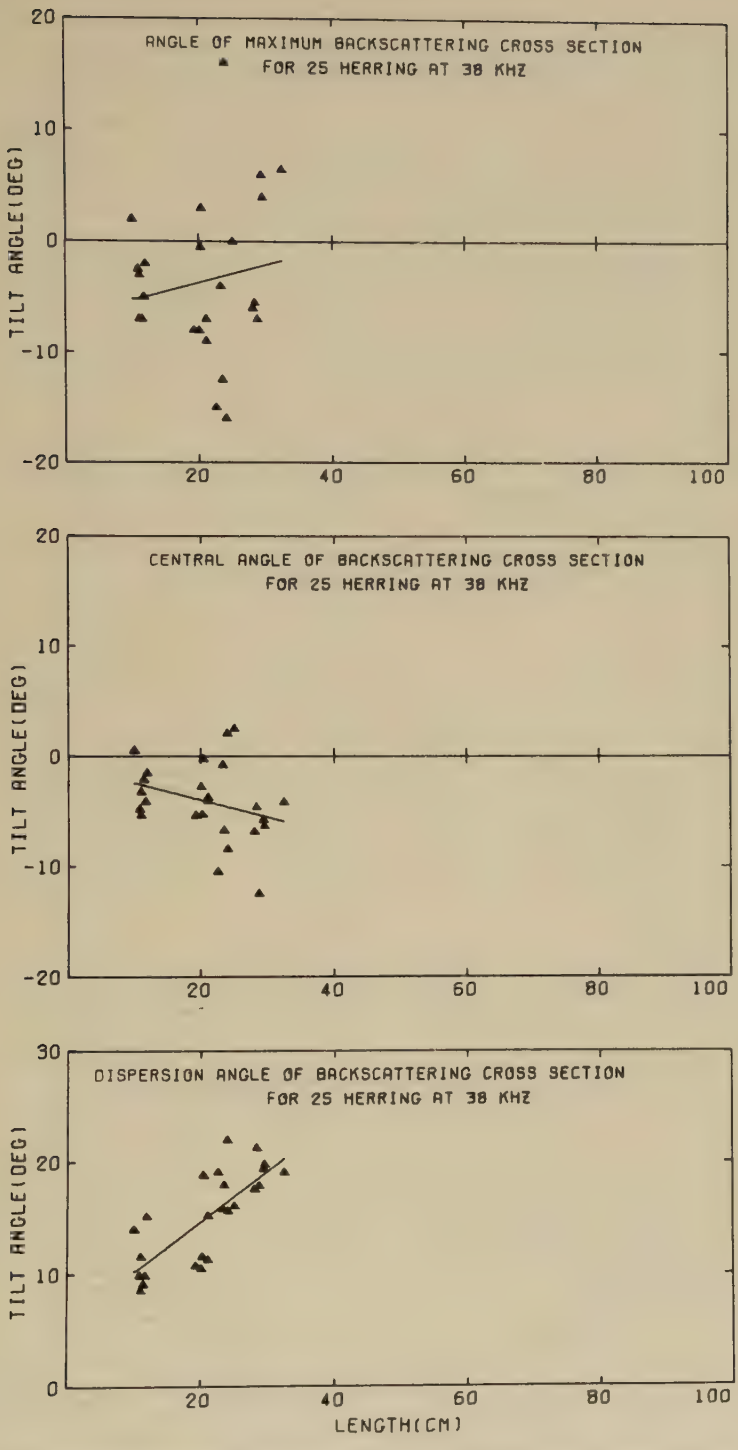

Fig. 7. Characteristic angular measures of measured dorsal aspect target strength functions of 25 herring at 38 kHz.

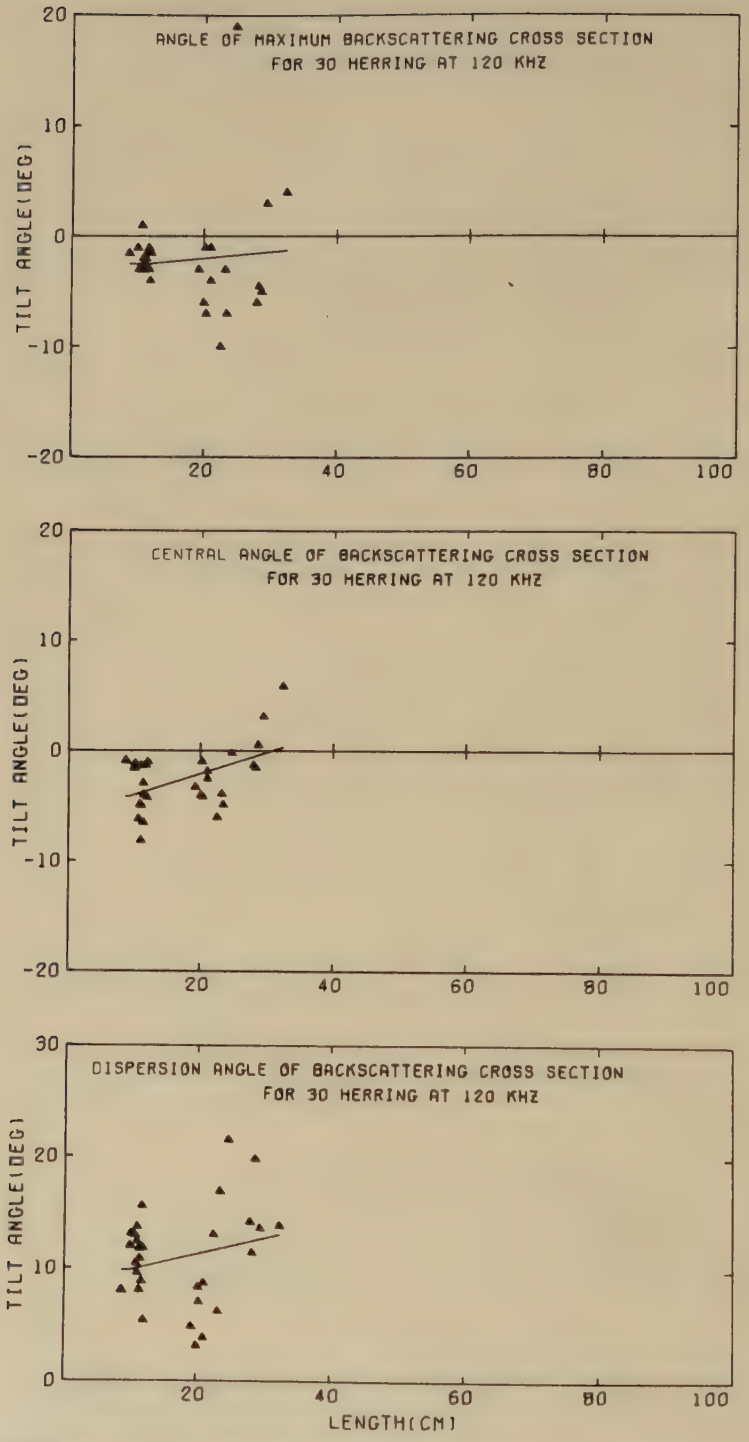

Fig. 8. Characteristic angular measures of measured dorsal aspect target strength functions of 30 herring at 120 kHz.

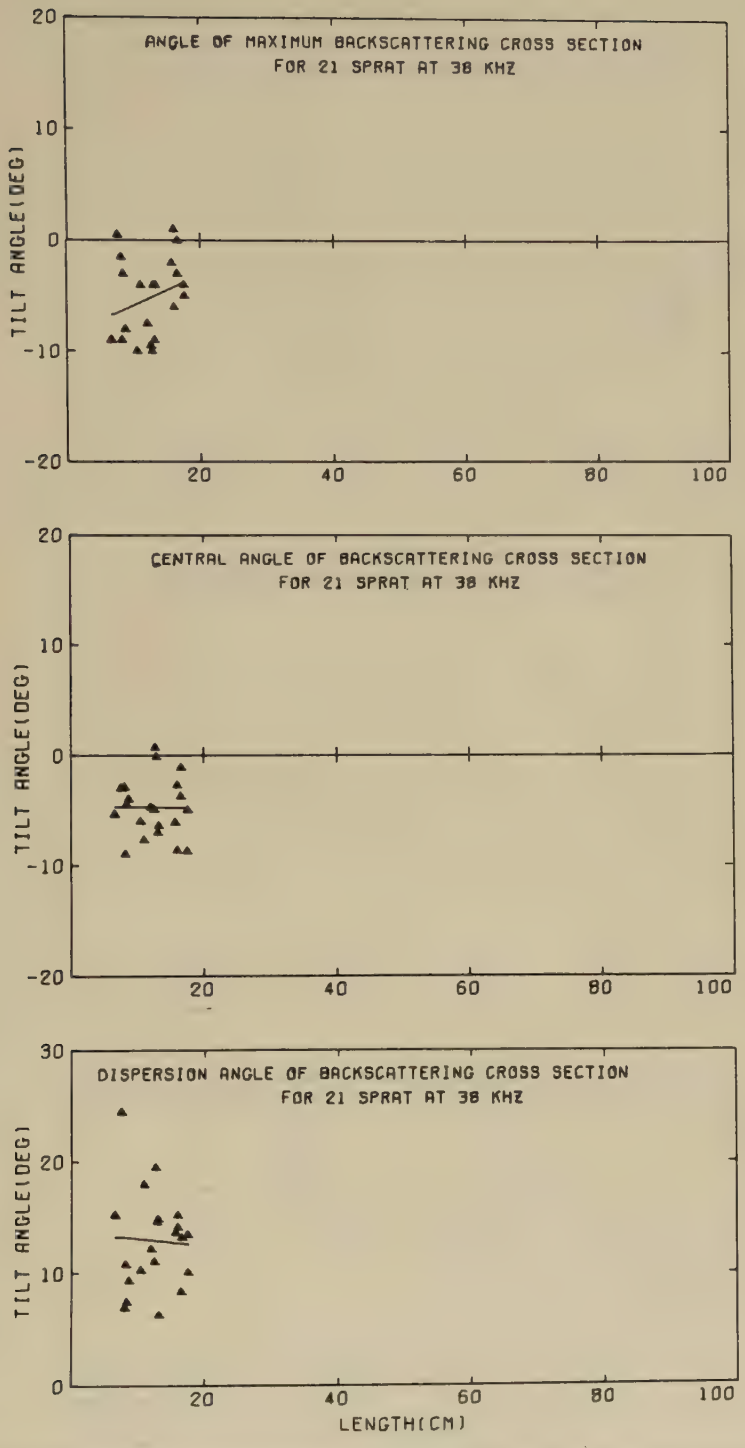

Fig. 9. Characteristic angular measures of measured dorsal aspect target strength functions of 21 sprat at 38 kHz.

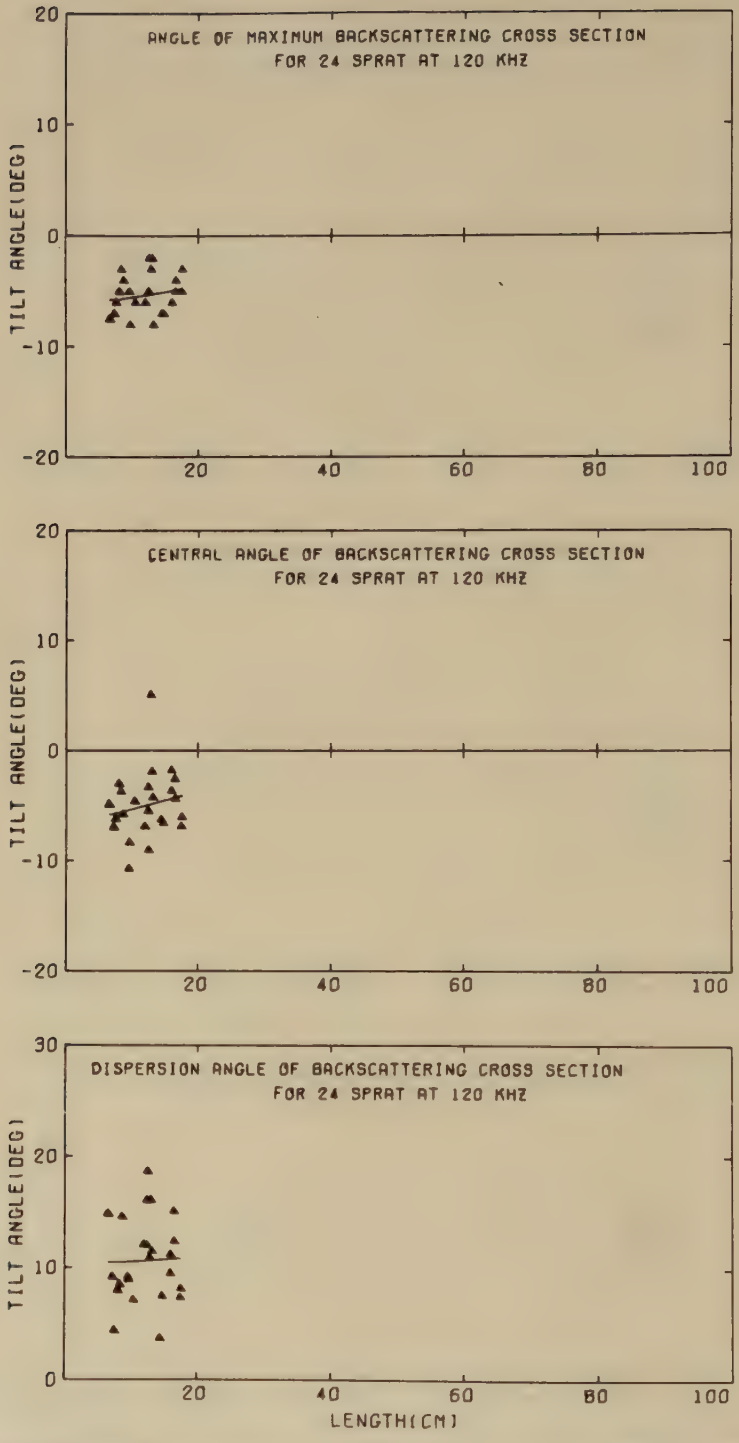

Fig. 10. Characteristic angular measures of measured dorsal aspect target strength functions of 24 sprat at 120 kHz.

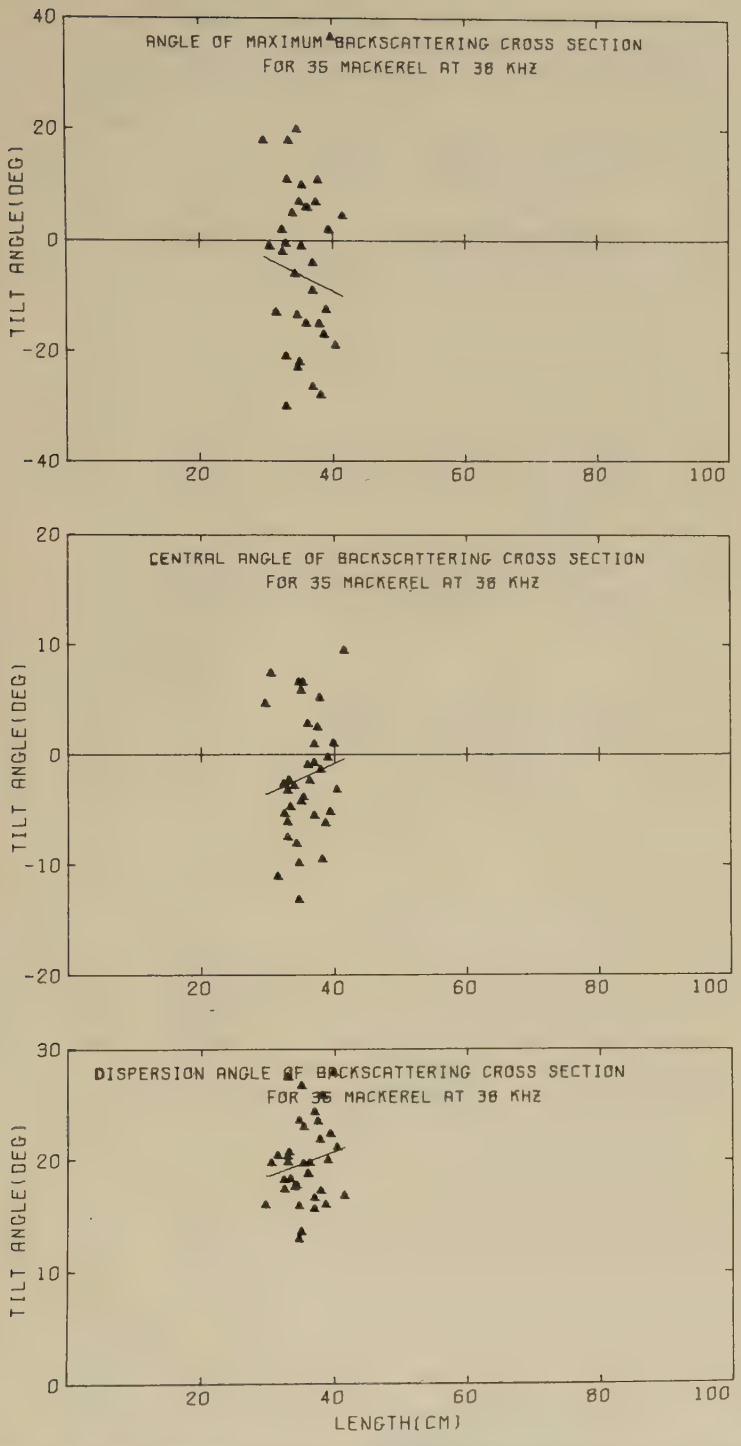

Fig. 11. Characteristic angular measures of measured dorsal aspect target strength functions of 35 mackerel at 38 kHz.

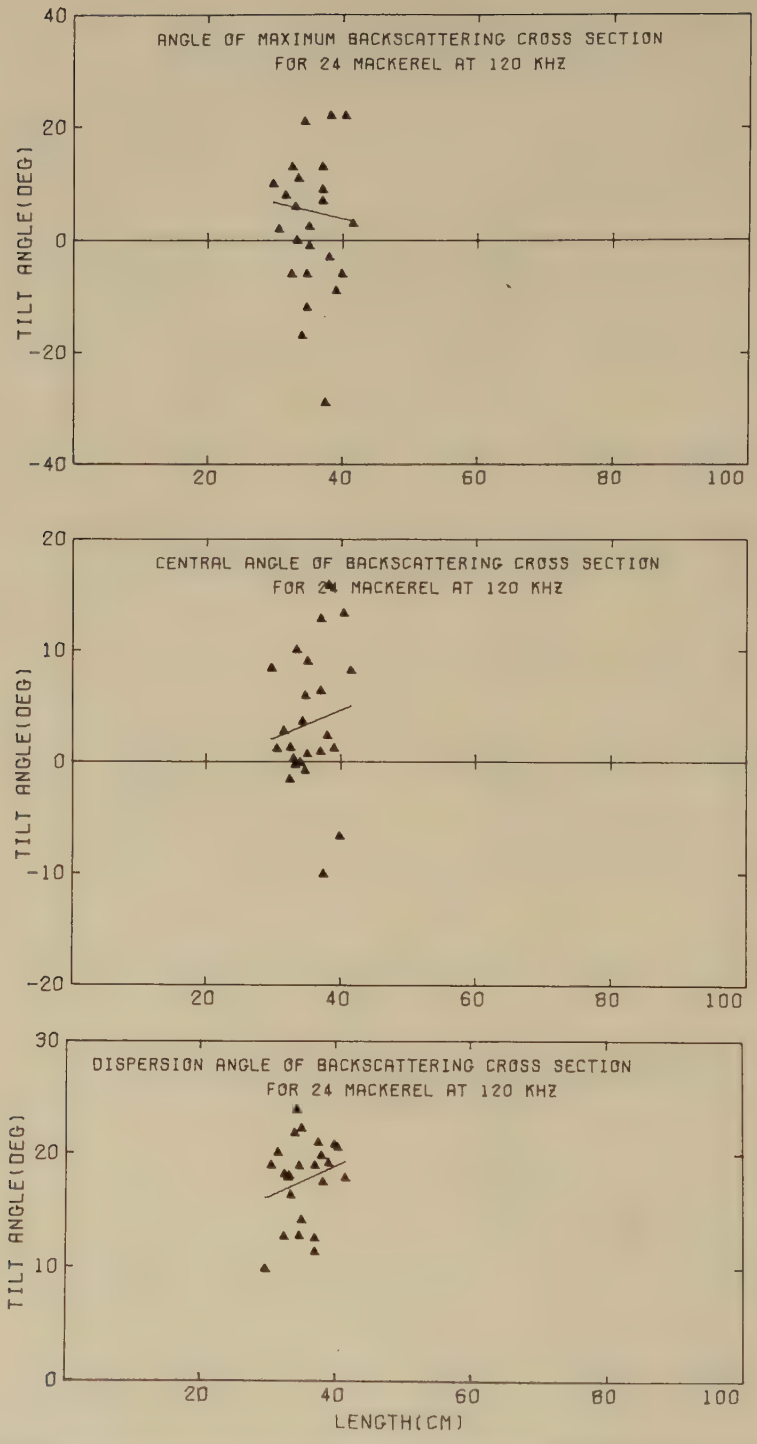

Fig. 12. Characteristic angular measures of measured dorsal aspect target strength functions of 24 mackerel at 120 kHz.

Table 2. Regression coefficients and mean, with statistical analyses, of α_0, the angle of maximum dorsal aspect backscattering cross section in the pitch plane.

Fish	Frequency (kHz)	Regression coefficient b_0				Regression coefficient b_1				Mean α_0			
		est	est(SE)	t	γ	est	est(SE)	t	γ	est	est(SE)	t	γ
Cod	38	–2.75	1.34	–2.04	0.04	–0.05	0.03	–1.80	0.08	–4.90	5.18	–0.94	0.35
Cod	120	–0.54	1.44	–0.38	0.71	–0 12	0.04	–2.99	$<10^{-2}$	–4.27	5.19	–0.82	0.42
Saithe	38	–2.12	0.90	–2.35	0.02	–0.04	0.02	–1.53	0.13	–3.34	3.29	–1.02	0.31
Saithe	120	–2.48	0.61	–4.08	$<10^{-3}$	–0.03	0.02	–1.77	0.08	–3.41	2.21	–1.54	0.13
Pollack	38	–2.01	2.20	–0.91	0.37	–0.02	0.07	–0.31	0.76	–2.66	4.58	–0.58	0.56
Pollack	120	–1.48	1.12	–1.32	0.20	–0.06	0.04	–1.57	0.12	–3.19	1.69	–1.89	0.07
Herring	38	–6.86	4.60	–1.49	0.15	0.16	0.21	0.77	0.45	–3.50	7.15	–0.49	0.63
Herring	120	–3.09	2.38	–1.30	0.20	0.06	0.12	0.47	0.64	–2.05	4.88	–0.42	0.68
Sprat	38	–8.51	2.88	–2.95	0.01	0.27	0.22	1.23	0.23	–5.10	3.60	–1.42	0.17
Sprat	120	–6.45	1.36	–4.73	$<10^{-3}$	0.10	0.11	0.93	0.36	–5.23	1.77	–2.96	0.01
Mackerel	38	7.40	33.7	0.22	0.83	–0.30	0.95	–0.32	0.75	–3.29	15.5	–0.21	0.83
Mackerel	120	7.55	29.7	0.25	0.80	–0.14	0.84	–0.17	0.87	2.52	12.4	0.20	0.84

Table 3. Regression coefficients and mean, with statistical analyses, of α_1, the central angle of the dorsal aspect backscattering cross section in the pitch plane.

Fish	Frequency (kHz)	Regression coefficient b_0				Regression coefficient b_1				Mean α_1			
		est	est(SE)	t	γ	est	est(SE)	t	γ	est	est(SE)	t	γ
Cod	38	–2.80	0.82	–3.43	$<10^{-2}$	–0.02	0.02	–1.09	0.28	–3.59	3.10	–1.16	0.25
Cod	120	–0.54	1.28	–0.42	0.68	–0.01	0.03	–0.42	0.68	–1.01	4.20	–0.24	0.81
Saithe	38	–2.82	0.67	–4.23	$<10^{-3}$	0.03	0.02	1.95	0.06	–1.67	2.46	–0.68	0.50
Saithe	120	0.24	0.90	0.27	0.79	–0.01	0.03	–0.44	0.66	–0.10	3.18	–0.03	0.98
Pollack	38	–1.07	1.42	–0.75	0.46	–0.03	0.05	–0.76	0.45	–2.10	2.97	–0.70	0.48
Pollack	120	1.93	1.29	1.49	0.14	–0.09	0.05	–2.07	0.04	–0.67	1.99	–0.34	0.74
Herring	38	–0.96	2.19	–0.44	0.66	–0.16	0.10	–1.55	0.14	–4.17	3.53	–1.18	0.25
Herring	120	–5.93	1.22	–4.87	$<10^{-3}$	0.19	0.06	3.03	$<10^{-2}$	–2.52	2.87	–0.88	0.39
Sprat	38	–4.56	2.24	–2.03	0.06	–0.02	0.17	–0.10	0.92	–4.78	2.70	–1.77	0.09
Sprat	120	–6.91	2.38	–2.91	0.01	0.16	0.19	0.87	0.39	–4.92	3.07	–1.60	0.12
Mackerel	38	–11.8	12.1	–0.97	0.34	0.28	0.34	0.81	0.42	–1.96	5.62	–0.35	0.73
Mackerel	120	–5.41	14.6	–0.37	0.72	0.25	0.41	0.61	0.55	3.51	6.15	0.57	0.57

Table 4. Regression coefficients and mean, with statistical analyses, of α_2, the angular dispersion of the backscattering cross section about the central angle in the pitch plane.

Fish	Frequency (kHz)	Regression coefficient b_0				Regression coefficient b_1				Mean α_2			
		est	est(SE)	t	γ	est	est(SE)	t	γ	est	est(SE)	t	γ
Cod	38	12.9	0.8	16.3	$<10^{-3}$	0.02	0.02	1.13	0.26	13.7	3.01	4.55	$<10^{-3}$
Cod	120	12.2	1.1	10.8	$<10^{-3}$	0.07	0.03	2.16	0.04	14.3	3.92	3.66	$<10^{-2}$
Saithe	38	8.7	0.7	12.3	$<10^{-3}$	0.12	0.02	6.14	$<10^{-3}$	12.5	3.25	3.86	$<10^{-3}$
Saithe	120	8.5	0.8	10.5	$<10^{-3}$	0.13	0.02	5.45	$<10^{-3}$	12.3	3.66	3.38	$<10^{2}$
Pollack	38	14.2	1.9	7.4	$<10^{-3}$	–0.05	0.06	–0.77	0.45	12.8	4.03	3.17	$<10^{2}$
Pollack	120	10.0	2.0	5.0	$<10^{-3}$	0.00	0.07	0.00	1.00	10.0	2.95	3.40	$<10^{-2}$
Herring	38	5.7	1.7	3.3	$<10^{-2}$	0.45	0.08	5.69	$<10^{-3}$	15.1	4.13	3.64	$<10^{-2}$
Herring	120	8.5	2.1	4.1	$<10^{-3}$	0.14	0.11	1.32	0.20	11.0	4.35	2.53	0.02
Sprat	38	13.6	3.7	3.7	$<10^{-2}$	–0.07	0.28	–0.23	0.82	12.8	4.40	2.90	0.01
Sprat	120	10.1	3.0	3.4	$<10^{-2}$	0.04	0.23	0.18	0.86	10.6	3.79	2.81	0.01
Mackerel	38	11.8	8.1	1.5	0.14	0.22	0.23	1.00	0.32	19.8	3.74	5.29	$<10^{-3}$
Mackerel	120	7.8	8.6	0.9	0.38	0.28	0.24	1.14	0.27	17.6	3.70	4.76	$<10^{-3}$

They are represented further by the condensations of results presented in Tables 5 and 6.

In Table 5 the regression coefficients and means of the several angle measures are classified by their consistency with one of two hypotheses. The null hypothesis H_0 asserts the identity or indistinguishability of the quantities with zero. The alternative hypothesis H_A denies this, asserting the nonvanishing nature of the quantities. The criterion for classification is that the significance level γ shall exceed 0.05 to uphold H_0 and be less than 0.05 to support H_A.

Table 5. Numbers of regression coefficients and means of angle measures consistent with the null or alternative hypotheses at the 0.05 level.

Angle measure	$\hat{b}_0$		$\hat{b}_1$		$\bar{\alpha}$	
	H_O	H_A	H_O	H_A	H_O	H_A
α_0	7	5	11	1	11	1
α_1	8	4	10	2	12	0
α_2	2	10	8	4	0	12

Table 6. Discrimination of regression coefficients and means of angle measures by their signs.

Angle measure	$\text{sgn}(\hat{b}_0)$		$\text{sgn}(\hat{b}_1)$		$\text{sgn}(\bar{\alpha})$	
	+	−	+	−	+	−
α_0	2	10	4	8	1	11
α_1	2	10	5	7	1	11
α_2	12	0	10	2	12	0

The lack of a trend in the maximum and central angles is evident from the results for the regression slope coefficient b_1 in Table 5. The null hypothesis is strongly upheld. Simple application of the binomial test attaches a confidence level of 0.997 to the consistency of b_1 with zero in the case of α_0 and a confidence of 0.98 in the case of α_1.

The same two angle measures are generally negative, however, as indicated by the sign analyses of Table 6. The negative character of maximum and central angle measures is evident from the results for the mean angle

measure $\overline{\alpha}$. Similar results for the regression intercept coefficient b_0 support this conclusion. The single exceptional datum for $\overline{\alpha}$ in Table 6 is that for mackerel at 120 kHz. Given the general upwards inclination, in the tail-to-head direction, of the gadoid and clupeoid swim bladder, which is probably the dominant scattering organ of these fishes, and the absence of a swim bladder in mackerel, it seems reasonable to distinguish the data by the presence or absence of a swim bladder. That the angles of maximum and central backscattering cross section are slightly negative, in the mean, for each non-mackerel fish, but apparently vanishing in the case of mackerel, may be regarded as a direct acoustical consequence of the described anatomical difference. An early observation of the acoustic manifestation of swim bladder inclination with respect to the imaginary fish centerline, to which the swim bladder axis is referred, was made by MIDTTUN and HOFF (1962).

The intrinsically positive character of the dispersion angle α_2 is confirmed by the sign analysis of $\overline{\alpha}$ in Table 6. This is supported by the positive regression intercept coefficient $\hat{b}_0$. The upwards trend of α_2 is observed in the positive regression slope coefficient $\hat{b}_1$ in Table 6, although not in the more stringent, but weaker analysis of Table 5. The physical interpretation of the increasing trend of mean dispersion angle with increasing fish length is that the dorsal aspect backscattering cross section or target strength in the pitch plane tends to be less concentrated as fish length increases. This conclusion appears plausible from inspection of the source data (FOOTE and NAKKEN 1978), although the magnitude of the length dependence of α_2 is not easily discerned from the data in this form.

Measures of the angular characteristics of target strength functions as computed in this paper do not seem to have been previously considered. The principal usefulness of the computations is expected to lie in considerations of the sort advanced in OLSEN (1979). Computations of angle measures cannot, however, supplant such measures of fish scattering strength as those considered in FOOTE (1978, 1979a–e, 1980a). These averaged measures of effective backscattering strength are essential to quantitative studies of fish abundance, whether assessed by typical echo sounders or by sector scanning sonars.

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Received 31 October 1979
Printed 2 June 1980

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